NEW AND CONFUSED SPECIES IN THE GENUS *NAVICULA* (BACILLARIOPHYCEAE) AND THE CONSEQUENCES OF RESTRICTIVE GENERIC CIRCUMSCRIPTION

Andrzej WITKOWSKI[1], Horst LANGE-BERTALOT[2] and Katarzyna STACHURA[3]

[1] Institute of Marine Sciences, University of Szczecin, Felczaka 3a, 71-412 Szczecin, Poland
[2] Botanical Institute, J.-W. Goethe University, Siesmayerstr. 70, D-60054 Frankfurt am Main, Germany
[3] Institute of Oceanography, University of Gdańsk, Piłsudskiego 46, 81-372 Gdynia, Poland

ABSTRACT — Electron microscopic investigations indicate that there are serious taxonomic problems with some taxa which, at a first glance seem to fit the restricted generic diagnosis of *Navicula*. Even if these taxa apparently resemble *Navicula* as typified by Patrick (1959; cf. Cox, 1979; Round *et al.*, 1990) under LM. SEM examination reveals several important morphological differences. Six different morphological groups have been distinguished within the genus *Navicula*. They differ with respect to stria structure, lineola shape, external central raphe endings, terminal raphe endings, position of the internal raphe fissures and cingulum structure. It remains to be decided whether subgenera should be created within the genus *Navicula*, or whether particular subgroups should be raised to generic rank. We think that future studies will provide further evidence of the heterogeneity of the genus *Navicula*. However, *N. bourrellyivera*, *N. hanseatica*, *N. rolandii*, *N. vaneei* and *N. witkowskii* are described here as new species which strictly conform to *Navicula* as typified by *N. tripunctata*.

RÉSUMÉ — Les études en microscopie électronique indiquent que les taxons qui, au premier abord, semblent correspondre à la diagnose d'une vision restreinte du genre *Navicula*, posent, en fait, des problèmes taxinomiques sérieux. Même si ces taxons ressemblent au genre *Navicula* tel qu'il fut typifié par Patrick (1959; cf. Cox, 1979; Round *et al.*, 1990) en microscopie optique, l'examen au microscope électronique à balayage révèle des différences morphologiques importantes. Sept groupes morphologiques différents ont été distingués au sein du genre *Navicula*. Ils diffèrent par la structure des striae, la forme des lineolae, les extrémités du raphe central, les extémités du raphe terminal, la position des fissures du raphe interne et la structure du cingulum. Il reste à décider si des sous-genres doivent être créés au sein du genre *Navicula*, ou si des sous-groupes particuliers doivent etre élevés au rang de genre. Nous pensons que des études futures apporteront des preuves supplémentaires de l'hétérogénéité du genre *Navicula*. Cependant, *N. bourrellyivera*, *N. hanseatica*, *N. rolandii*, *N. vaneei* et *N. witkowskii* sont décrits ici comme des espèces nouvelles strictement conformes au genre *Navicula* tel qu'il a été typifié par *N. tripunctata*. (Traduit par la Rédaction)

KEY WORDS: Bacillariophyceae, diatoms, *Navicula*, Naviculaceae, new species, microalgae, morphology, taxonomy.

INTRODUCTION

The circumscription of *Navicula* Bory (Naviculaceae, Bacillariophyceae) has varied greatly. In addition to the Section Lineolatae, *Navicula* has included several other sections and an undetermined number of taxa which do not neccessarily possess naviculoid valve outlines (e.g. Cleve, 1894-1895; Peragallo & Peragallo, 1897-1908; Hustedt, 1927-1966; Krammer & Lange-Bertalot, 1986). With establishment of the segregate genera *Haslea* (Simonsen, 1974), *Proschkinia* (Karayeva, 1978b) and *Lyrella* (Karayeva, 1978a), however, circumscription of *Navicula* became more restricted. This process has continued in two ways: either by creating new genera e.g. *Parlibellus* by Cox (1988); or by resurrecting genera whose member species were placed in *Navicula* [e.g. *Placoneis* Mereschkowsky (Cox, 1987a) and *Sellaphora* Mereschkowsky (Mann, 1989)]. Round *et al.*, (1990); Lange-Bertalot & Metzeltin (1996), Lange-Bertalot *et al.*, (1996), and Witkowski *et al.*, (1997) have provided further refinement. Patrick (1959) typified *Navicula* with *Navicula tripunctata* (O.F. Müller) Bory and Cox (1979) provided a detailed description of *N. tripunctata* and emended the generic circumscription of *Navicula*. Subsequently Round *et al.* (1990) and Round (1996) strongly recommended that *Navicula* be used in a restricted sense *i.e.* only for taxa belonging to the former Section Lineolatae, which includes *N. tripunctata*.

Recent studies, however, reveal that even this concept of *Navicula* includes a heterogeneous assemblage of taxa, as already suggested by Cox (1979). Chloroplast structure and valve morphology as observed in LM are of little significance. Only SEM studies allow particular subgroups within *Navicula* to be distinguished. Based upon valve morphology Lange-Bertalot *et al.* (1996) segregated *Navicula capitata* Ehrenberg and related taxa into a new genus, *Hippodonta*.

Over the last few years strong opposition arose against placing taxa in the genus *Navicula* which do not fit the diagnosis of the former Section Lineolatae. Since the publication of Round *et al.* (1990) the genus *Navicula* has become particularly ambiguous (*i.e. Navicula sensu stricto* and *sensu lato*). In *Navicula sensu stricto* taxa with the following characteristics are included: boat shaped valves, lineolate striae, central external raphe endings simple, apical endings hooked to one side, internal raphe slit running obliquely in raised ribs and without visible central pores and two lateral plastids (Cox, 1979; Round *et al.*, 1990; Round, 1996). *Navicula sensu lato* includes groups of species which do not conform with the above criteria. A provisional solution for "homeless" taxa was recently proposed by Lange-Bertalot *in* Lange-Bertalot & Moser (1994) who established *Naviculadicta* for taxa which belong neither in *Navicula sensu stricto* nor in other established genera. This approach could be used until an adequate classification accomodates all "homeless" taxa.

In the present paper results of our studies on the diatom genus *Navicula* are introduced. In this paper, which originates from a project dealing with diatom flora of the marine littoral, our attention was focused on taxa which are routinely identified as representatives of *Navicula* in the light microscope. It was our intention to show that *Navicula*, in the sense of the former Section Lineolatae with *N. tripunctata* as the type is still heterogenous genus.

MATERIAL AND METHODS

Predominantly surface sediment samples from brackish-water and marine littoral localities from various geographic regions were studied (Table 1). The surface sediments from the Gulf od Gdańsk and Puck Bay (Poland) were irregularly sampled during 1991-1993, but at least once a quater (Stachura & Witkowski, in press). During 1993 selected stations along the shore of the Gulf of Gdańsk and Puck Bay including salt marsh area were sampled at monthly intervals. Samples from the Mecklenburg Bay originated from 13 cores (up to 6 m long). In all, several hundreds of samples from around the world were studied, but for this particular paper only 26 sites were chosen. Samples were selected to cover all possible environmental conditions with respect to salinity, climate and substrate.

Table. 1. Samples studied, localities and collections.

No.	Sampling site	Geographic region	Substrate	Country	Collection
1.	Władysławowo	Puck Bay Baltic Sea	salt marsh	Poland	Witkowski
2.	Gulf of Gdańsk	Baltic Sea	surface sediments	Poland	Witkowski
3.	Puck Bay	Baltic Sea	surface sediments	Poland	Witkowski
4.	Mecklenburg Bay	Baltic Sea	fossil sediments	Danmark/ Germany	Witkowski
5.	Kattegat	Baltic Sea	surface sediments	Danmark	Witkowski
6.	Bear Island	Barents Sea	tidal flat sediments	Norway	Witkowski/ Lange-Bertalot
7.	Franz Joseph Land	Arctic Ocean	*Laminaria* sp.	Russia	Witkowski
8.	fjord near Narvik	Norwegian Sea	sediment	Norway	Reichardt
9.	Weser River		sediment	Germany	Lange-Bertalot
10.	Reckerta River	NW Germany	sediment	Germany	Lange-Bertalot
11.	mouth of the River Weser	North Sea Bremerhaven	tidal flat	Germany	Brockmann
12.	La Rochelle	Atlantic Ocean	sediment	France	Lange-Bertalot
13.	Vila Franco da Campo	Atlantic Ocean Azores	algal mat rock pool	Portugal	Lange-Bertalot
14.	Mississippi Delta	Gulf of Mexico	sand	USA	Lange-Bertalot
15.	Campeche	Gulf of Mexico	sediment	Mexico	Lange-Bertalot
16.	Lake Mir	Mediterranean	sediment	Croatia	Lange-Bertalot

17.	Coast of Crete	Mediterranean	sediment	Greece	Reichardt
18.	Eilat	Red Sea	sediment	Israel	Reichardt
19.	Dar-es-Salam	Indian Ocean	sediment	Tanzania	Moeller (Copenhagen)
20.	Tonga harbour	Indian Ocean	harbour	Tanzania	Reichardt
21.	Coast of Kenya	Indian Ocean	sediment	Kenya	Reichardt
22.	Qurum Beach	Gulf of Oman	calcareous sand	Oman	Lange-Bertalot
23.	St. Gilles-les-Bains	Indian Ocean	algal mat	La Réunion	Reichardt
24.	Fiji Islands	Pacific Ocean	sediment	Fiji	Foged (Copenhagen)
25.	Kok-tao Island	Pacific Ocean	sand	Thailand	Lange-Bertalot
26.	Drake's Bay	California	sand	USA	Reichardt

The samples were cleaned by boiling in concentrated HCl, washed several times with distilled water, and boiled in H_2SO_4 with small amounts of KNO_3 added at *ca* 15 min. intervals. Other samples were boiled in concentrated hydrogen peroxide in order to remove organic matter. After washing several times with distilled water, the samples were dried onto coverglasses. Coverglasses were attached to slides with Naphrax.

Light microscopic studies were carried out by means of a Leitz Diaplan microscope with 63/1.4 PlanAPO oil immersion objective. SEM studies were performed by means of a Hitachi S 4500. All the SEM stubs are deposited at the Botanical Institute of J.-W. Geothe University, Frankfurt am Main in collection Lange-Bertalot.

RESULTS

The results of our study are arranged into seven sections. In six sections particular groups of taxa which shows consistent characteristics are introduced. In the seventh one a mixed group of taxa is presented. There is no doubt that they differ from *Navicula sensu stricto*, but so far they have only been found as single entities so that, at present, no grouping is possible. Newly described taxa are compared with other related species of *Navicula sensu stricto* (Table 2). Finally each of the six groups is presented by listing the most important characters (Table 3).

Navicula sensu stricto (Figs 1-14, 23-32, 35-38, 88-93)

Navicula sensu stricto encompasses *ca* 150 species inhabiting freshwater and *ca* 50 ones living in brackish water and the marine environment. Our observations indicate that there are still numerous undescribed taxa, belonging to *Navicula sensu stricto* inhabiting marine littoral. All the taxa included in *Navicula sensu stricto* possess characters found in *N. tripunctata*. The most important features of *Navicula sensu stricto* are given in Table 2. They are characterized by striae composed of numerous lineolae, simple central external raphe endings, hooked apical raphe endings, internal raphe fissure running obliquely in raised ribs and cingulum composed of open bands. Here five new taxa are being described. Three of the following new species belong to an apparently closely related group of taxa

living predominantly in brackish waters e.g. *N. slesvicensis* Grunow, *N. meniscus* Schumann, *N. rhynchotella* Lange-Bertalot, *N. peregrina* (Ehr.) Kützing and *N. kefvingensis* (Ehr.) Kützing. The remaining two taxa *N. witkowskii* and *N. rolandii* are related to *N. salinarum* Grunow. For at least three of the new taxa, single specimens were already depicted by various authors (e.g. Germain, 1981; Krammer & Lange-Bertalot, 1986) but were lumped within the more prominent species, for example *N. rhynchocephala* Kützing. Without a doubt, all of these taxa belong to *Navicula sensu stricto* showing all diagnostic characteristics with *N. tripunctata*.

Navicula bourrellyivera **Lange-Bertalot, Witkowski & Stachura sp. nov. Figs 1-6.**
Type: Praep. No. Eu-PL 72 in Coll. Lange-Bertalot, Botanical Institute University of Frankfurt
Type locality: Salt marsh, Władysławowo, Puck Bay, Poland (*leg.* A. Witkowski, 1993).

Latin diagnosis. *Valvae lanceolatae vel modice lineari-lanceolatae apicibus cuneatis plusminusve longe protractis ad extremum acutius ad obtusius rotundatis. Longitudo 30-55 µm, latitudo 10-12 µm. Raphe filiformis ad modice lateralem poris centralibus distincte signatis. Area axialis angusta, area centralis fere parva ad modice amplam, transverse rectangularis vel lanceolata. Striae transapicales radiantes ad apices versus convergentes, 9-11 in 10 µm, lineolae crassae apparentes, 20-21 in 10 µm.*

Etymology. This species is dedicated to our late colleague and exemplary international phycologist Pierre Bourrelly. The epithet *bourellyivera* was chosen because the combination *Navicula bourrellyi* Manguin (Manguin, 1960) is in use for a taxon which does not belong to the genus *Navicula*, but must be transferred to another, as yet undefined genus.

Diagnosis. Valves lanceolate to moderately linear-lanceolate with moderately acutely rounded, more or less protracted apices, 30-55 µm long, 10-11 µm wide. Raphe filiform to moderately lateral, external central raphe endings distinctly expanded, terminal raphe endings strongly curved in the same direction. Axial area linear, narrow, central area somewhat variable in shape, transversely rectangular to lanceolate, usually asymmetrical. Transapical striae radiate in the middle, becoming slightly convergent towards apices, 9-11 in 10 µm. Striae composed of distinct lineolae, 20-21 in 10 µm.

Distribution and ecology. It occurs in brackish waters of the Baltic and North Sea. Usually infrequent but sometimes abundant in local populations. This species also has been encountered infrequently and with few individuals in freshwater, in particular rivers under eutrophic conditions and with higher conductivity.

N. bourrellyivera might have been overlooked in the past or confused with *Navicula rhynchocephala*. It belongs to ■ group of taxa which are closely related morphologically (see below) and live under lower to higher brackish water conditions. Among this group *N. hanseatica* Lange-Bertalot & Stachura has the most similar combination of characteristics in common with *N. bourrellyivera*. However, the taxa are easy to distinguish from one another if associated in the same samples, as is the case in the type locality. They differ in valve breadth, number of striae in 10 µm and shape of the central area (Table 2).

Navicula hanseatica Lange-Bertalot & Stachura sp. nov. Figs 23-27
Type: Praep. No. Eu-PL 72 in Coll. Lange-Bertalot, Botanical Institute University of Frankfurt
Type locality: Salt meadow, Władysławowo, Puck Bay, Poland (*leg.* A. Witkowski, 1993).

Latin diagnosis. *Valvae lanceolatae apicibus quoad individua minutissima simpliciter cuneatis quoad individua media ad maxima plusminusve longe protractis ad extremum acute*

rotundatis nonumquam capitatis vel subcapitatis. Longitudo 30-70 µm, latitudo 12-15 µm. Fissurae raphis paulo laterales poris centralibus crasse signatis. Area axialis angusta, area centralis ampla plerumque transverse rectangulata. Striae transapicales radiantes ad apices versus convergentes, 8-9 in 10 µm. Lineolae comparate conspicue crassae apparentes, 20-21 in 10 µm.

Diagnosis. Valves lanceolate with protracted and acutely rounded ends in middle sized and longer specimens, and simply cuneate ends only in the smallest specimens. Ends never capitate or subcapitate. Length 30-70 µm, breadth 12-15 µm. Raphe fissures moderately lateral with distinctly expanded central pores. Axial area narrow, central area large mostly transversely expanded. Striae radiate but at the ends convergent, 8-9 in 10 µm. Lineolae comparatively very coarse, 20-21 in 10 µm. SEM: Central raphe fissures endings outside into large central pores with hooked processes (similar but less distinctly than in *Navicula peregrina*). Valve face flat, the sternum does not form an elevated rib outside (Figs 37-38).

Etymology. The name of the new species is derived from "Hanse" ■ powerful, medieval trade organization which existed in the Baltic Sea region.

Distribution and ecology. It is frequent to abundant in brackish waters of the marine littoral in Europe and river estuaries.

New species is identical with *N. rhynchocephala* var. *amphiceros sensu* Germain (1981, fig. 69: 2) *N. rhynchotella* (cf. Lange-Bertalot 1993) is similar in many characteristics, morphological and ecological, however, the valves are not tapering to the ends but are protracted more abruptly in all stages of the cell cycle. Furthermore the smallest valves have no cuneate ends (Table 2).

Navicula rolandii Wunsam, Witkowski & Lange-Bertalot sp. nov. Figs 88-93.
Type: Praep. No. E-Lok 103 in Coll. Lange-Bertalot, Botanical Institute University of Frankfurt.
Type locality: Lake Mir, Croatia, the Mediterranean, (*leg.* S. Wunsam, 1995).

Latin diagnosis. *Valvae lineari-ellipticae apicibus curte cuneatis ad extremum fere obtuse nec distincte acute rotundatis, 30-47 µm longae, 10-11 µm latae. Raphe filiformis ad mediam versus declinata in poros centrales incrassatos dense positos inter se. Fissurae terminales curte hamatae unilateraliter ut generaliter in Navicula. Area axialis angustissima, area centralis parva fere variabilis ad instar. Striae transapicales irregulariter undulatae conspicue radiantes ad apices versus parallelae vix convergentes, in media nonnullae striae abbreviatae interpositae apparentes, 10-11 in 10 µm. Lineolae difficiliter discernandae, 35 in 10 µm.*

Diagnosis. Valves linear-elliptical with more or less cuneate, rather obtusely than acutely rounded apices, 34-47 µm long, 10-11 µm wide. Raphe filiform, external central raphe endings distinct, very close to each other. Terminal raphe endings somewhat declined and strongly curved to the same side. Axial area very narrow, central area small, variable in shape formed by irregular interposition of shorter striae. Transapical striae strongly radiate in the middle and parallel close to the apices, 10-11 in 10 µm. Lineolae difficult to discern with LM. 35 in 10 µm.

Etymology. This taxon is dedicated to our friend and colleague Roland Schmidt, phycologist and ecologist in Mondsee/Salzburg, Austria.

Distribution and ecology. The taxon is only known (in high numbers) from the type locality. It seems to be confined to brackish and marine habitats but has been overlooked or confused with other taxa in the past.

This species is very similar to the complex of taxa around *N. salinarum*, and less similar when compared with *N. witkowskii* (Table 2).

***Navicula vaneei* Lange-Bertalot sp. nov. Figs 28-32.**

Type: Praep. E-Lok 82 in Coll. Lange-Bertalot, Botanical Institute J. W. Goethe University, Frankfurt am Main.
Type locality: River Reckerta near "Heiliges Meer" in northwestern Germany (*leg.* Ingeborg Krause, August 1993)

Latin diagnosis. *Valvae lanceolatae apicibus plerumque non protractis raro minime protractis, ad extremum obtuse rotundatis, 40-80 µm longae, 11-13 µm latae. Fissurae raphis modice laterales poris centralibus crasse signatis. Area axialis modice anguste linearis, area centralis distincte asymmetrica apparens, transverse rectangulata ad transverse ellipticam. Striae transapicales radiantes, denique convergentes, 8-10 in 10 µm. Lineolae valde crassae apparentes, 20-24 in 10 µm. SEM: Pori centrales ampli sed paulo hamati.*

Diagnosis. Valves lanceolate with ends which are, regularly, not protracted or, exceptionally, indistinctly protracted, apices obtusely rounded, 40-80 µm long, 11-13 µm broad. Raphe fissures moderately lateral with coarsely marked central pores. Axial area linear and moderately narrow, central area distinctly asymmetric, transversely rectangular to elliptic. Transapical striae radiate, convergent at the apices, 8-10 in 10 µm. Lineolae comparatively coarse, 20-24 in 10 µm. SEM: The large central pores with short, hook-like processes (Figs 35-36) are similar to *N. peregrina*.

Etymology. This taxon is dedicated to our friend and colleague Gert van Ee, phycologist and ecologist in Haarlem, Holland. He was the first to ask for the real identity of this taxon among the complex of several similar species around *Navicula rhynchocephala*.

Distribution. Until recently only known from several localities in Europe.

Ecology. It occurs infrequently, but locally abundantly in eutrophic inland waters, or freshwaters near sea coasts with moderately high conductivity.

This species was probably observed by other authors also in the past but not discerned from similar taxa, such as: *N. rhynchotella*, *N. slesvicensis*, *N. peregrina* and *N. meniscus*. For example it was not distinguished from *N. rhynchocephala* by Krammer & Lange-Bertalot (1986, fig. 31: 1-2). Germain (1981, fig. 69: 4-6) identified it as *N. rhynchocephala* var. *elongata* A. Mayer. *N. pseudolanceolata* Lange-Bertalot is (less) similar, but, has a distinctly different autecology, occurring, in oligotrophic slightly acid waters with very low conductivity.

***Navicula witkowskii* Lange-Bertalot, Iserentant & Metzeltin sp. nov. Figs 7-11.**
Type: Praep. ■ 5894(1) in Coll. Brockmann, Natur-Museum Senckenberg, Frankfurt am Main
Type locality: Mouth of the River Weser, Bremerhaven (6.4.1934, *leg.* (?) C. Brockmann)

Latin Diagnosis. *Valvae lanceolatae vel elliptico-lanceolatae apicibus protractis rostratiformibus ad extremum obtuse rotundatis. Longitudo, 20-45 µm, latitudo, 9-12 µm. Fissurae raphis modice sive distincte laterales poris centralibus fere distantes inter se. Area axialis modice anguste linearis, area centralis variabilis quoad amplitudinem, circularis ad ellipti-*

cam. Striae transapicales valde radiantes ad apices versus parallelae denique convergentes, 10-12 in 10 µm. Lineolae fere difficiliter discernandae in microscopo photonico, 33 in 10 µm.

Diagnosis. Valves lanceolate or elliptical-lanceolate with protracted rostrate ends and obtusely rounded apices, 20-45 µm long, 9-12 µm broad. Raphe fissures moderately to more distinctly lateral with marked central pores in a somewhat distant position to each other. Axial area moderately narrow, linear, central area variable in extension, circular to elliptical. Transapical striae strongly radiate but parallel and finally convergent near the apices, 10-12 in 10 µm. Lineolae not easy to discern with LM, though not more than about 33 in 10 µm.

Etymology. This taxon is dedicated to our friend, colleague and co-worker, A. Witkowski from the University of Szczecin, Institute of Marine Sciences.

Distribution and ecology. It occurs frequently in brackish water of European coasts and river estuaries, whereas rarely in freshwaters with moderate to higher conductivity.

Up to now this taxon was either completely neglected and/or probably confused with *N. salinarum* or *N. digitoradiata* (Gregory) Ralfs (var. *rostrata* Hustedt), but agrees with *N. digitoradiata sensu* Brockmann (1950, fig. 2: 3). It occurs often with *N. salinarum* and *N. digitoradiata*, but is easy to distinguish in such associations (Table 2).

Table 2. Morphometric characteristic of newly described and related *Navicula* taxa.

Species	Length in µm	Width in µm	Striae in 10 µm	Lineolae in 10 µm	Shape	Apices	Central area
N. tripunctata (O. F. Müller) Bory	30-70	6-10	10-11	32	linear-lanceolate	obtusely rounded	rectangular
N. bourellyivera Lange-Bertalot, Witkowski & Stachura	30-55	10-12	9-11	20-21	lanceolate/ linear-lanc.	Acutely rounded	rectangular/ lanceolate
N. hanseatica Lange-Bertalot & Stachura	30-72	12-15	8-9	20-21	lanceolate	protracted acutely rounded	transversely expanded
N. rolandii Wunsam, Witkowski & Lange-Bertalot	30-47	10-11	10-11	35	linear-elliptical	cuneate obtusely rounded	small irregular
N. vaneei Lange-Bertalot	40-80	11-13	8-10	20-24	lanceolate	obtusely rounded	rectangular/ elliptical asymmetric
N. witkowskii Lange-Bertalot, Iserentant & Metzeltin	20-45	9-12	10-12	33	lanceolate/ elliptic-lanceolate	protracted rostrate	variable circular/ elliptical
N. digitoradiata (Gregory) Ralfs	25-80	7-28	7-14	32	lanceolate/ linear – lanceolate	obtusely rounded lanceolate	small circular
N. kefvingensis (Ehr.) Kützing	44-90	10-18	7-8.5	25-27	lanceolate	obtusely rounded	rectangular
N. meniscus Schumann	35-70	13-20	7-8	22	lanceolate	acutely rounded	rectangular expanded
N. peregrina (Ehr.) Kützing	40-180	10-30	5-61	8-20	lanceolate	obtusely rounded	rectangular/ elliptical

N. rhynchocephala Kützing	35-80	9-14	7-12	20-25	lanceolate	obtusely rounded	rectangular/ elliptical
N. rhynchotella Lange-Bertalot	35-60	10-16	8-11	20-25	lanceolate	protracted slightly capitate	transversely expanded
N. salinnarum Grunow	20-40	8-12	13-17	40	lanceolate	protracted slightly capitate	circular
N. slesvicensis Grunow	25-60	8-11	8-9	25	lanceolate	obtusely rounded	rectangular

The *Navicula cancellata* Donkin group (Figs 39-53)

Description: Valve faces and mantles not distinctly separated, but continuously strongly arched. Valve outlines linear-elliptical with broadly rounded apices. Raphe straight, central external endings deflected to the same side, close to each other. Internal raphe fissures in central position without raised siliceous sternum (Figs 58-59, 72). Terminal raphe endings strongly to moderately hooked to the same side, unlike in *Navicula sensu stricto* not in a polar but in a subpolar position (Fig. 45). Axial area narrow, central area relatively large. Transapical striae bold, composed of fine, regularly spaced lineolae. Girdle broad, composed of heteromorphic open bands.

This is a group of marine taxa with heavily silicified valves and broadly rectangular frustules in girdle view (Figs 41-43, 48-50, 52-53). Besides *N. cancellata*, *N. apiculata* Brébisson, *N. bipustulata* A. Mann, *N. crucifera* Grunow, *N. inflexa* Gregory, *N. mediterranea* Cleve & Brun, *N. northumbrica* Donkin, *N. retusa* Donkin, several until now undescribed taxa also belong in this group. Due to their comparatively broad girdle, taxa belonging to this group are rarely observed in valve view.

The *Navicula distans* W. Smith group (Figs 60-66)

Description: Frustules broadly rectangular in girdle view, valve faces slightly curved along apical axis. Valve outlines linear lanceolate with acutely rounded apices. Valve face (in SEM) flat in the middle, becoming arched towards apices. Raphe straight, external central raphe endings distinctly expanded. Terminal raphe endings curved to the same side. They continue up to the edge of the apex (Fig. 73). Internal raphe fissures distinctly deflected to one side of the raised raphe sternum terminating in a small helictoglossa. The central nodule is stauros-like, a shortened transapical bar (Fig 76). Axial area lanceolate, central area variable, mostly large, rectangular. The striae are composed of apically elongated, densely spaced slit-like foramina outside (Figs 60-62, 64-66). Internally they are positioned in comparatively very deep depressions (Fig. 74). Areolae on the interior seem to be much shorter than their external foramina (Figs 73-76). No internal occlusions with hymenes have been observed so far. Girdle composed of few (4) closed bands. The broad valvocopula has pectinate siliceous outgrowths (Fig. 63).

Species in this small group possess heavily silicified frustules, and include *N. distans* W. Smith and varieties, *N. pennata* A. Schmidt, probably *N. fortis* (Gregory) Ralfs, *N. longa* (Gregory) Ralfs and varieties and *N. spuria* Cleve. These are marine taxa with large and

robust cells, with the exception of *N. distans* var. *borealis* Grunow, the taxa are rather rarely reported.

The taxa included in this group occur in littoral marine environments. *N. distans* var. *borealis* occurs abundantly along European coasts up to the arctic Bear Island. *N. spuria* is reported predominantly from the warmer coasts e.g. the Mediterranean and Africa (Foged, 1975; Giffen, 1971). *N. fortis*, *N. longa* and *N. pennata* have been reported from European and American coasts of the Atlantic Ocean (A. Schmidt 1874, A. Schmidt *et al.*, 1874-1959; Peragallo & Peragallo, 1897-1908; Gemeinhardt, 1935; Hustedt, 1955).

The *Navicula platyventris* Meister group (Figs 15-22)

Description: Valve surface as observed in SEM is flat. In *N. platyventris* occurs a shallow depression along the raphe sternum. Raphe straight, external central raphe endings distinct, point-like. Internal central raphe endings continuous (Figs 78, 80). Terminal raphe endings strongly curved to the same side. Internal raphe fissures in central position. Unlike *Navicula sensu stricto*, the raphe sternum does not form a raised rib. Transapical striae are composed of S-shaped, sometimes irregular lineolae (Figs 77, 79). The areolae at the valve interior are covered with thin hymenes. The girdle is composed of four open bands. The valvocopula possesses short siliceous outgrowths (Fig. 78).

This is a small group of taxa which includes *N. platyventris* Meister, and *N. tropicoidea* Witkowski, Metzeltin & Lange-Bertalot. SEM examination will reveal whether or not *N. tropica* Meister, *N. raphoneis* Cleve and *N. perrhombus* Hustedt (Figs 94-99) belong to this group.

N. platyventris is predominantly distributed in warm regions of all oceans (e.g. Meister, 1935; Foged, 1975, 1987; Bafana & Witkowski, 1995), whereas *N. tropicoidea* has only been recorded from the type locality, namely Bear Island (Metzeltin & Witkowski, 1996).

The *Navicula starmachioides* Witkowski & Lange-Bertalot group (Figs 82-85)

Description: Valve faces arched along apical axis. Unlike *Navicula sensu stricto* there is no abrupt transition from valve face to mantle, but a gradual transition is observed over a steep slope. Raphe straight, exactly central in the middle of the valve, but slightly displaced to the valve margin near the apices. Internal raphe fissure deflected to one side of the raised raphe rib. This is similar to the conditions in *Navicula sensu stricto.* External central raphe endings simple, dot-like, terminal raphe endings simple, forming short slits or terminal pores indistinctly deflected to the same side. Transapical striae composed of slit-like foramina, areolae internally occluded by thin hymenes. At the apices a variable number of circumpolar areolae occur. The girdle is composed of four open, relatively broad bands (Figs 86-87).

This is a group of marine and brackish-water taxa, which are easily confused with those belonging to the group around *Navicula cancellata* and the newly established genus *Hippodonta* Lange-Bertalot, Metzeltin & Witkowski.

The *Navicula wasmundii* Witkowski, Metzeltin & Lange-Bertalot group
(Figs 100-110)

Description: Frustules rectangular in girdle view. Valves lanceolate to linear-lanceolate, with acutely to broadly rounded apices. Valve face flat without distinct change to the valve mantle. Raphe straight with simple, dot-like external central endings. Terminal raphe endings strongly hooked to the same side. Internal raphe fissures straight, central, within the raphe sternum which does not form a raised rib. Axial area very narrow, linear, central area small, rectangular. Transapical striae composed of simple lineolae. Areolae open externally as apically oriented slits and are internally covered by thin hymenes. Striae are regularly composed of only a few (2-3) lineolae. In each stria one or two lineolae occur along the valve margin and only one along the raphe. Lack of lineolae in the middle part of the valve gives an impression as if the taxa under consideration possess lateral areas (Figs 111-116). Our observations indicate, however, that the structure is different from lateral area recorded in *Fallacia* Stickle & Mann, *Lyrella* Karayeva (cf. Round *et al.*, 1990) or *Fogedia* (Witkowski *et al.*, 1997). On the other hand, observations on broken specimens indicate that the valve face is composed of two siliceous layers (Metzeltin & Witkowski, 1996).
This group is composed of only — so far as is known — a few small celled marine taxa which have often been confused with the complex around *Navicula perminuta* Grunow.

Other questionable groups in *Navicula sensu stricto*

Navicula pseudopima Hustedt and its forma *lanceolata* Hustedt (cf. Simonsen 1987, fig. 599:1-3) are without doubt members of the Lineolatae, but, are they really members of *Navicula sensu stricto*? Round *et al.* illustrate within *Navicula* (1990, p. 567, fig. j, k) a taxon which seems to belong to the group in question. Except an extremely convex valve shape with strong mantles, they possess a peculiar conopeum, but lack the typical hooked terminal raphe fissures. These features are unknown in the 150-200 species of *Navicula* which conform with the type species *N. tripunctata*. These typical *Navicula* taxa are characteristic elements of freshwater and brackish waters. However, the "atypical" groups under consideration here are elements of brackish to fully marine habitats, and not freshwaters.

Other examples of Naviculae Lineolatae which may not belong to *Navicula sensu stricto* are *Navicula gracilis* var. *recurva* Meister (Figs 67-68), and *N. flagellifera* Hustedt (Figs 33-34, 69-70). We compared our LM photos of *N. gracilis* var. *recurva* with SEM micrographs (phot. W. Güttinger) and found a channel-like to keel-like construction above the valve sternum. This feature is completely unknown in freshwater *Navicula* taxa. At first glance *N. flagellifera* possesses the typical valve features of *Navicula sensu stricto* When observed under SEM it reveals a peculiar construction of apices and internal raphe fissures somewhat similiar to *N. distans* and to *Trachyneis* Cleve (Figs 69-70). These and other examples will be published elsewhere.

DISCUSSION

SEM examination of the morphology of *Navicula* spp. even adopting the restrictive generic delimitation of Round *et al.* (1990) has revealed that, contrary to the recently expressed conviction (Round, 1996), at least six discrete groups can be distinguished. Our studies indicate that strict application of the generic diagnosis has the consequence of excluding from *Navicula* many taxa of the "Lineolatae". Only one of the groups (Table 3) under discussion here may be considered a subgenus in *Navicula sensu stricto*, *i.e.* the *N. starmachioides* group.

The designation of *N. tripunctata* as type of *Navicula* by Patrick (1959), emended by Cox (1979) has brought about important consequences for the circumscription of the genus. Subsequently Round *et al.* (1990) have emended the traditional diagnosis (Krammer & Lange Bertalot, 1986) of the Naviculaceae. Among diatomists there exists a distinct tendency to reject genera which do not represent "homogenous groups" of taxa. Following this strict concept, only the *N. starmachioides* group can be included in *Navicula sensu stricto* as an infrageneric rank, e.g. as a subgenus. The only important differences between *N. starmachioides* and *N. tripunctata* are the apical raphe endings and the heteromorphic girdle elements. All the other groups distinguished here (Table 3) show more significant morphological differences from the diagnosis of *Navicula*. In particular this is seen in the following features: position of the internal raphe fissures, structure of the striae, and the girdle.

In general the internal raphe fissures of *Navicula sensu stricto* open laterally and are positioned within a thin, raised siliceous rib on the sternum. In *N. platyventris* and in *N. wasmundii* the internal raphe fissures have a central position continuously and resemble recently delimited genera, *i.e. Fogedia* (Witkowski *et al.*, 1997) and *Hippodonta* (Lange-Bertalot *et al.*, 1996). However, they differ from *Fogedia* and *Hippodonta* by having strongly curved apical raphe endings, which are typical for *Navicula*.

In the *N. distans*, group the raphe internal structure resembles *Navicula sensu stricto* but there is a distinct difference. In addition the structure is reminiscent of *Trachyneis*, especially at the apices and in the middle (e.g. Round *et al.*, 1990; Medlin, 1991). Two features provide the most pronounced evidence in a support of this: a distinct stauroid silica accumulation at the central nodule and the internal raphe central ends. The transapically expanded central nodule can also be observed with LM. The terminal raphe ends of a group around *N. distans* also very much resemble those in *Trachyneis* and in *Rhoiconeis* Grunow (Round *et al.*, 1990; Medlin, 1991). However, there are also important differences between a group around *N. distans* and *Trachyneis* the most important of which is the stria structure.

The most prominent feature of *Navicula* apart from the boat-like outline in light microscope, is the structure of the striae, which are composed of apically elongated slits, the so-called lineolae (e.g. Cox, 1979, 1987b; Cox & Ross, 1981; Krammer & Lange-Bertalot, 1986; Round *et al.*, 1990; Round, 1996). The taxa we have studied with respect to this feature show some variability. In *Navicula tripunctata* and numerous related taxa lineolae are slit-like foramina. The most similar structure is exhibited by the *N. starmachioides* and *N. wasmundii* groups. *N. platyventris* shows a modification in form of S-curved foramina. The striae of species in the *N. distans* group have a different fine structure: externally the areolae open as very thin, densely spaced slits, while internally

they lie in deep depressions between two raised transapical costae (virgae). The internal width of the striae (depressions = alveoli) seem to be smaller than that of the external foramina. This feature is possibly observed even at different focus planes with LM. At upper focus, the striae are distinctly broader than at lower focus.

The girdle structure is also variable. *Navicula sensu stricto* and the *N. distans* and *N. platyventris* groups have the same principle type of girdle construction. Copulae are open, plain bands, while valvocopulae have pectinate outgrowths. Their length, however, is different and varies from very short or even missing in *Navicula sensu stricto* (see Cox, 1987b, 1995) through intermediate in *N. platyventris* to long outgrowths in *N. distans*. The girdles of *N. cancellata*, *N. starmachioides* and *N. wasmundii* possess similar stuctures and are composed of two different types of bands. Medlin (1991) uses the term heteromorphic girdle in such cases. She observed such girdles in *Rhoiconeis* and *Trachyneis*.

Interesting is a comparison of the *N. starmachioides* group with the newly established genus *Hippodonta*. Superficially both taxa resemble each other, especially with respect to the apical raphe endings, girdle construction and the presence of a peculiar "horse teeth" arrangement of foramina at the apices. In the light of the generic diagnosis of *Navicula*, the *N. starmachioides* group may be included in *Navicula*, whereas *Hippodonta* does not fit the diagnosis. Their discrimination in LM may be difficult. The key to solve this problem may be their different salinity requirements. *Hippodonta* comprises predominantly fresh — to slightly brackish water species, whereas the *N. starmachioides* group contains more brackish water and fully marine forms.

CONCLUDING REMARKS

The results of our study show inevitably that, despite efforts taken to clear the taxonomic problems within *Navicula sensu stricto* the aim of recognising a homogenous group of taxa has not yet been attained. We were able to vindicate our suspicion that, even within *Navicula sensu stricto*, there are several groups of species, which in light of a restricted generic diagnosis cannot be placed in the genus *Navicula*. The taxa which, based on LM observations, apparently belong to *Navicula*, studied with the aid of SEM have to be excluded from this genus if we follow the generic diagnosis. In this paper we illustrate six subgroups within *Navicula sensu stricto*, only one of which, *i.e.* the *N. starmachioides* group, in our opinion may be recognized as a subgenus of *Navicula*. Since we anticipate that more subgroups will be found in the future, we do not propose taxonomic changes at the generic level. It might be more appropriate to emend the generic diagnosis than to create new small genera, but it would not be an easy task.

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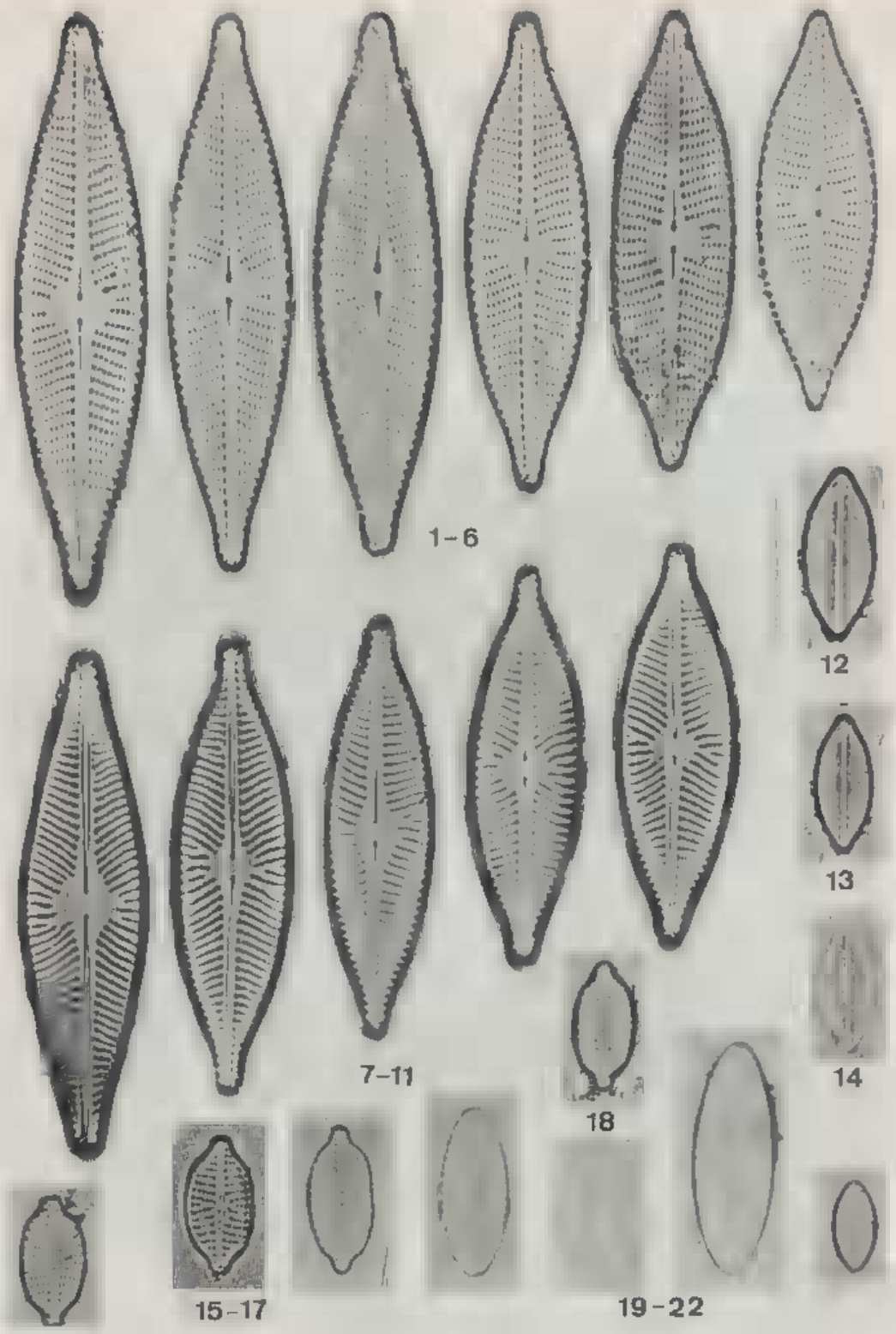
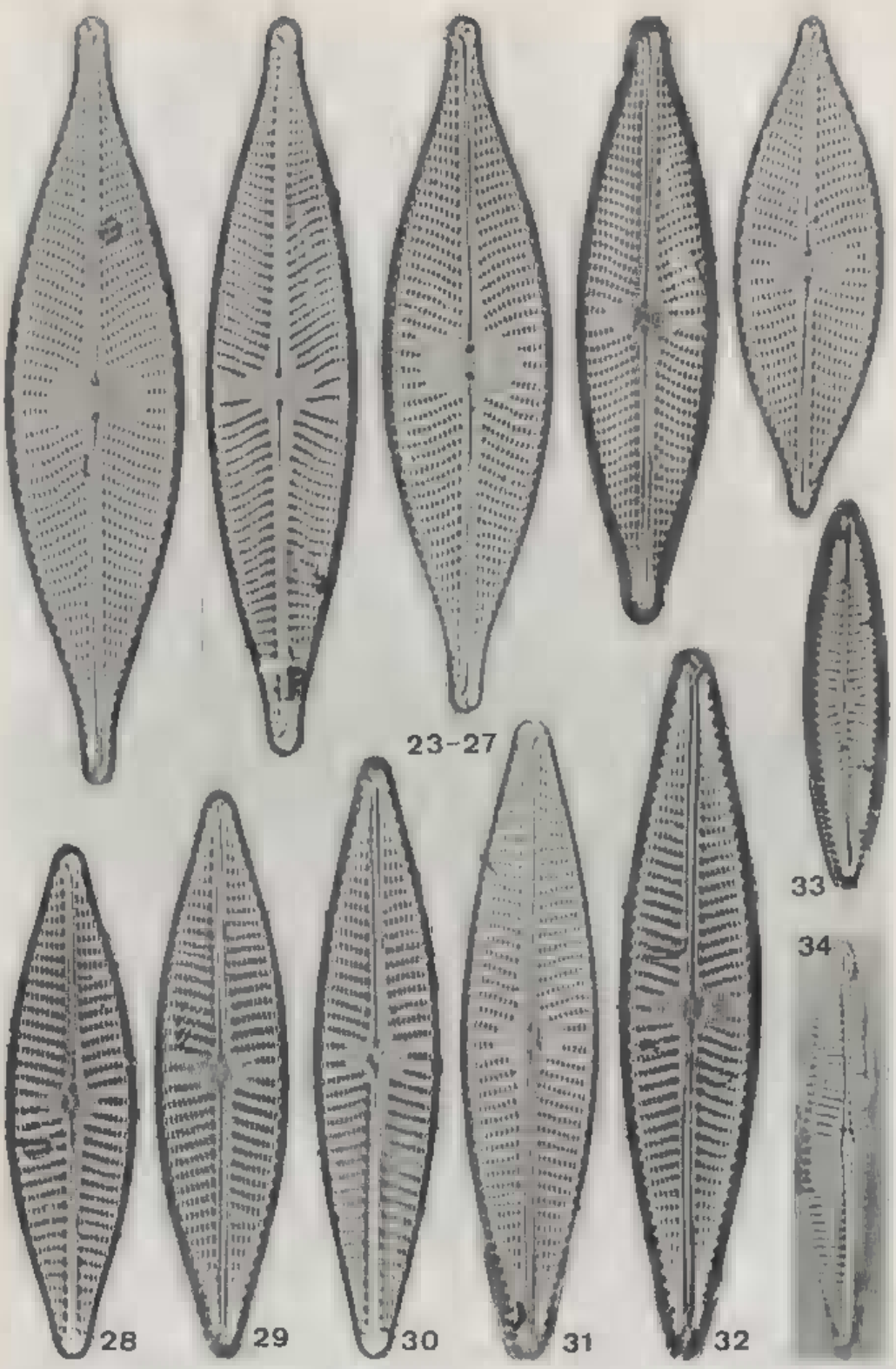
Table 3. The characteristic features of groups distinguished within *Navicula sensu stricto*

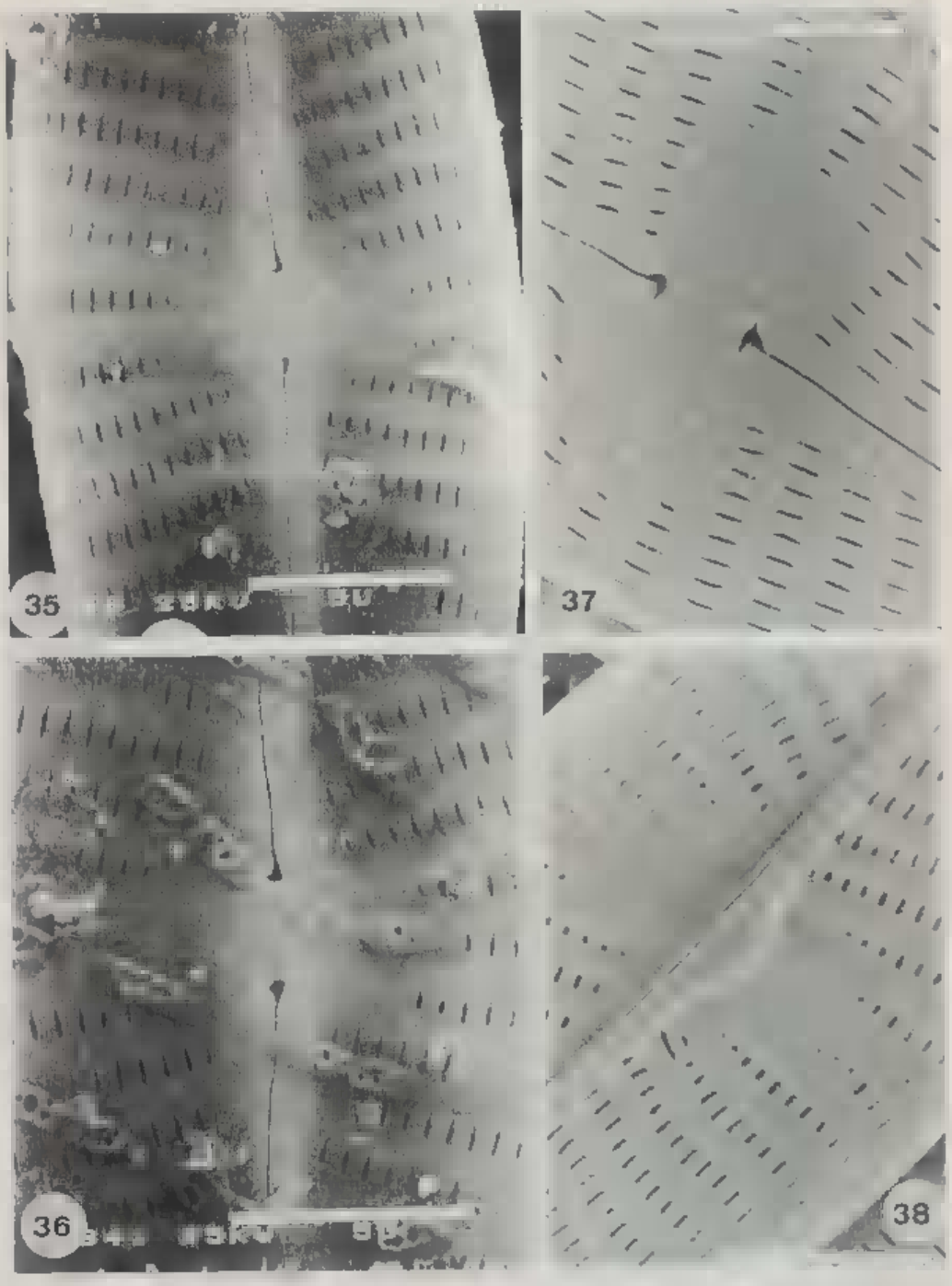
Taxonomic group	Shape of lineolae	Striae	Central raphe endings	Terminal raphe endings	Raphe rib on sternum	Internal raphe fissure	Internal central raphe endings	Cingulum
Navicula Section Naviculatae	slit-like	numerous lineolae	simple, filiform	hooked in polar position	present	deflected	discontinuous	open bands
N. cancellata group	slit-like, (fine)	numerous lineolae	deflected	hooked in subpolar position	absent	central	discontinuous	open bands
N. distans group	slit-like, (fine)	numerous lineolae	expanded	deflected	present	deflected	discontinuous	broad, with pectinate outgrowths
N. platyventris group	S-shaped	numerous lineolae	simple, filiform	hooked	absent	central	continuous	open with outgrowths
N. starmachioides group	slit-like	numerous lineolae	expanded	simple or slightly deflected	present	deflected	discontinuous	broad, open bands
N. wasmundii group	slit-like	2-3 lineolae	simple, filiform	hooked or deflected	absent	central	discontinuous	narrow, open bands



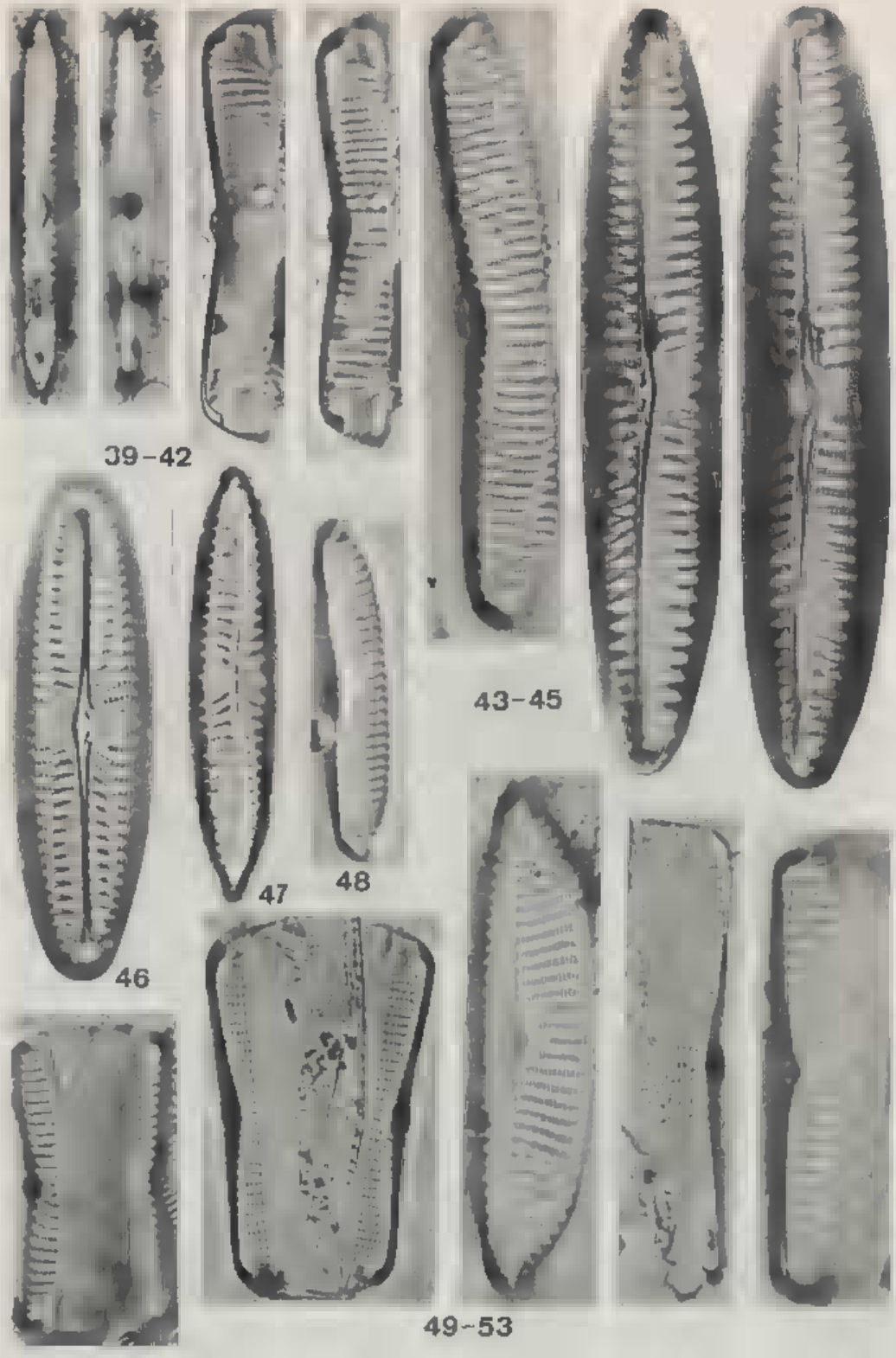
Figs 1-21. Figs 1-6. *Navicula bourrellyivera*, specimens from the salt marsh in Władysławowo, holotype slide. Figs 7-11. *Navicula witkowskii*, specimens from North Sea tidal flats, holotype slide. Figs 12-14. *Navicula viminoides*, specimens from the Mississippi Delta. Figs 12-13. The same valve at different magnification. Figs 15-18. *Navicula platyventris*. Fig. 15. Specimen from Fiji Islands. Fig. 16. Specimen from the Gulf of Oman. Fig. 17. Specimen from Kenya. Fig. 18. Specimen from South Africa. Figs 19-22. *Navicula tropicoidea*, specimens from Bear Island. Scale bar in Fig. 1 = 10 µm for Figs 1-11; 13-21, scale bar in Fig. 12 = 10 µm for Figs 12, 22.



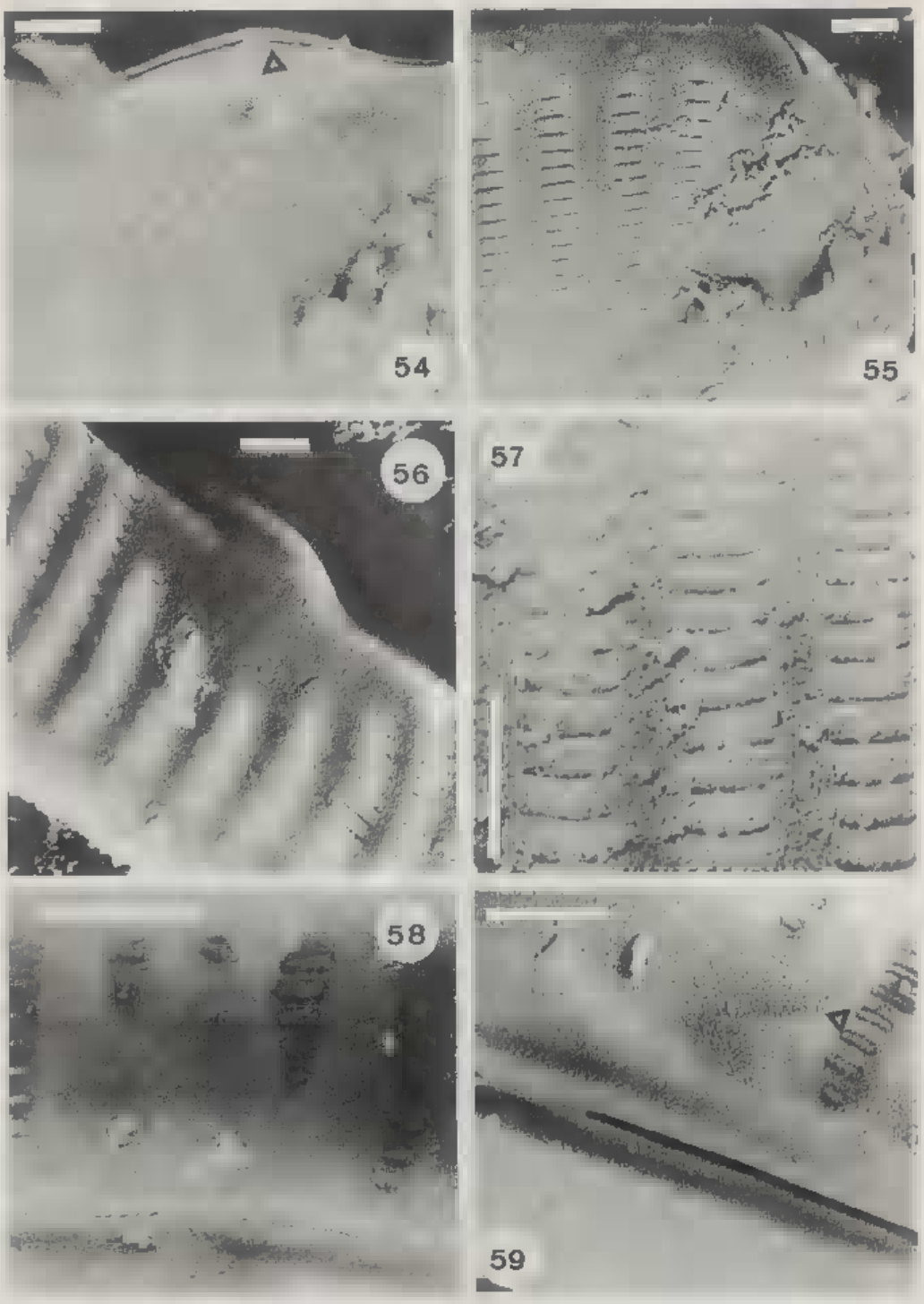
Figs 23-34. Figs 23-27. *Navicula hanseatica*, specimens from salt marsh in Władysławowo, holotype slide. Figs 28-32. *Navicula vaneei*. Figs 28-30 and 32. Specimens from River Reckerta, northwestern Germany, holotype slide. Fig. 31. Specimen from River Weser, sample No 1052, coll. Hustedt. Figs 33-34. *Navicula flagellifera*, specimens from the Mississippi Delta. Scale bar = 10 µm.



Figs 35-38. Figs 35-36 *Navicula vaneei*, SEM. Figs 35-36. Valve face, specimens from the type locality. Fig. 35. Middle part of the valve exterior showing central raphe pores and central area. Fig. 36. Central area of the specimen covered with regularly structured particles (siliceous skeletons of unknown organisms?). Figs 37-38. *Navicula hanseatica*. Specimens from the type locality. Fig. 37. Middle part of the valve exterior at higher magnification showing central raphe endings. Fig. 38. Valve interior typical of *Navicula sensu stricto*, characteristic position of the raphe sternum with raphe fissures. Scale bars = 5 µm.

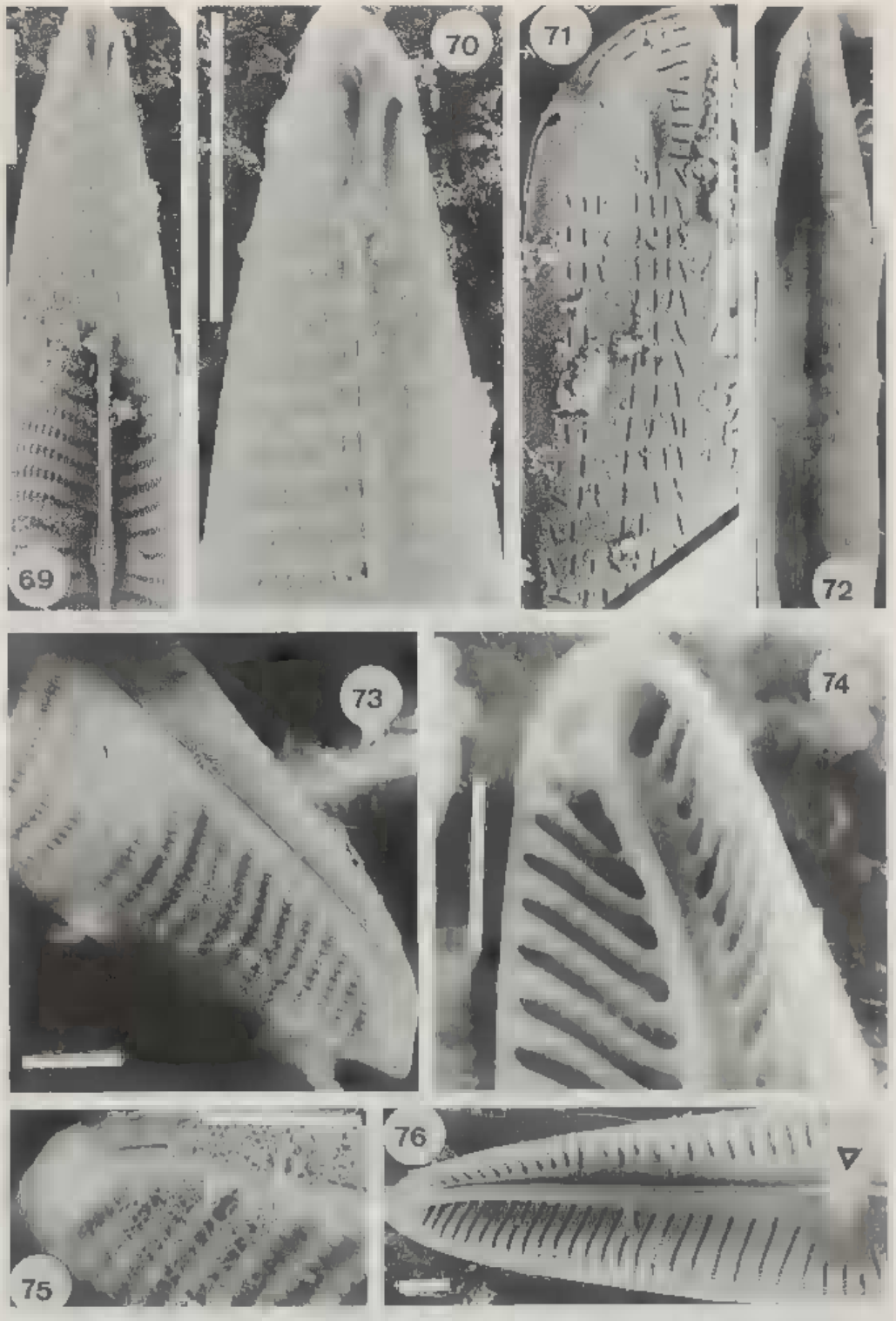


Figs 39-53. *Navicula cancellata* group. Figs 39-42. *Navicula* aff. *retusa*, specimens from the Mississipi Delta. Fig. 39-40. Valve face view of the same specimen at different foci. Fig. 39. Focus on the central nodule. Fig. 40. Focus at the raphe terminal endings (arrowhead). Figs 41-42. Girdle view of the same specimen at different foci showing the presence of an unusual central nodule (cf. SEM micrographs Figs 54, 56). Figs 43-46, 53. *Navicula cancellata*. Figs 43, 53. Specimens from Bear Island. Fig. 44-45. Specimens from the coast of Crete, Mediterranean Sea. Fig. 46. Specimen from Narvik. Figs 47-49. *Navicula bipustulata*. Fig. 47. Specimen from Narvik. Figs 48-49. Specimens from the Gulf of Gdańsk. Figs 50-51. *Navicula crucifera*. Fig. 50. Specimen from Drake's Bay, north of San Francisco, California. Fig. 51. Specimen from La Rochelle, Atlantic coast, France. Fig. 52. *Navicula northumbrica*, specimen from La Rochelle, Atlantic coast, France. Scale bar = 10 µm.



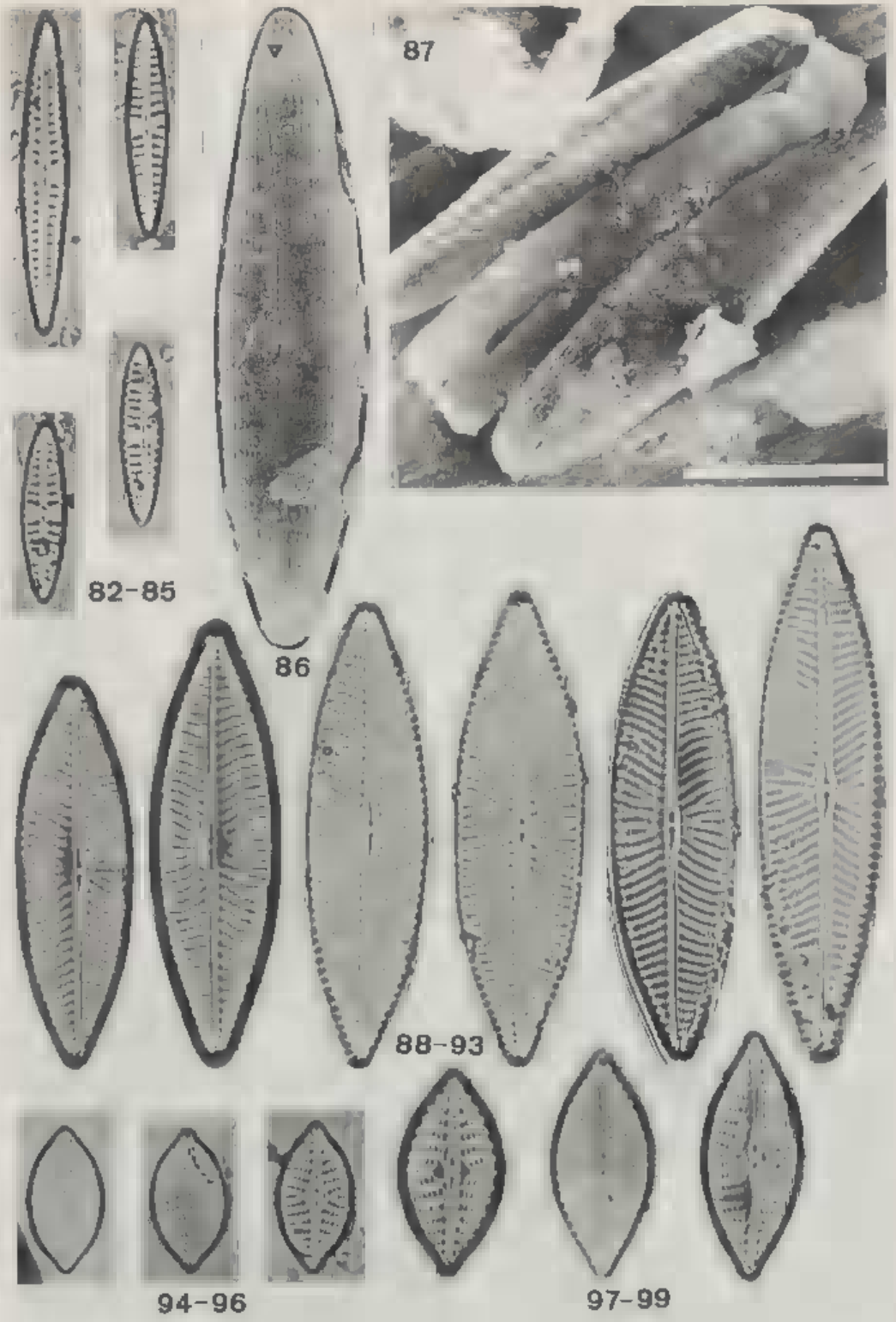
Figs 54-59. SEM. *Navicula cancellata* group. Figs 54-59. *Navicula* aff. *retusa*, SEM, specimens from the Mississippi Delta. Figs 54, 56. Middle part of the valve exterior. Fig. 54. External central raphe endings (arrowhead). Fig. 56. Central nodule in the girdle view. Fig. 55. External view of valve apex in girdle view. Fig. 57. External areolae openings at higher magnification. Figs 58-59. Interior of the valve centre showing centrally positioned raphe slits and the absence of a raised sternum. Note the presence of hymenate occlusions (arrowhead). Scale bars = 1 µm.

Figs 60-68. Figs 60-66. *Navicula distans* group. Figs 60-61, 63. *Navicula distans* var. *borealis*. Figs 60-61. The same specimen at different foci. Fig. 60. Focus on the valve interior. Fig. 61. Focus on the external valve surface. Note different appearance of the striae and of the central raphe pores. Fig. 63. Centre of the pectinate valvocopula of *N. distans* var. *borealis*. Figs 60-61, 63. Specimens from Bear Island. Fig. 62. *Navicula pennata*. Figs 64-65. *Navicula* aff. *spuria*. Figs 62, 64. Specimens from Drake's Bay, north of San Francisco, California. Fig. 65. Specimen from the Indian Ocean coast, Kenya. Fig. 66. *Navicula longa var. irregularis*, specimen from the Gulf of Campeche. Figs 67-68. *Navicula gracilis var. recurva*. Fig. 67. Specimen from the Azores, Atlantic Ocean. Fig. 68. Specimen from La Rochelle, Atlantic coast, France. Scale bar in Fig. 60 = 10 µm for Figs 60-61, 63; scale bar in Fig 62. = 10 µm for Figs 62, 64-68.

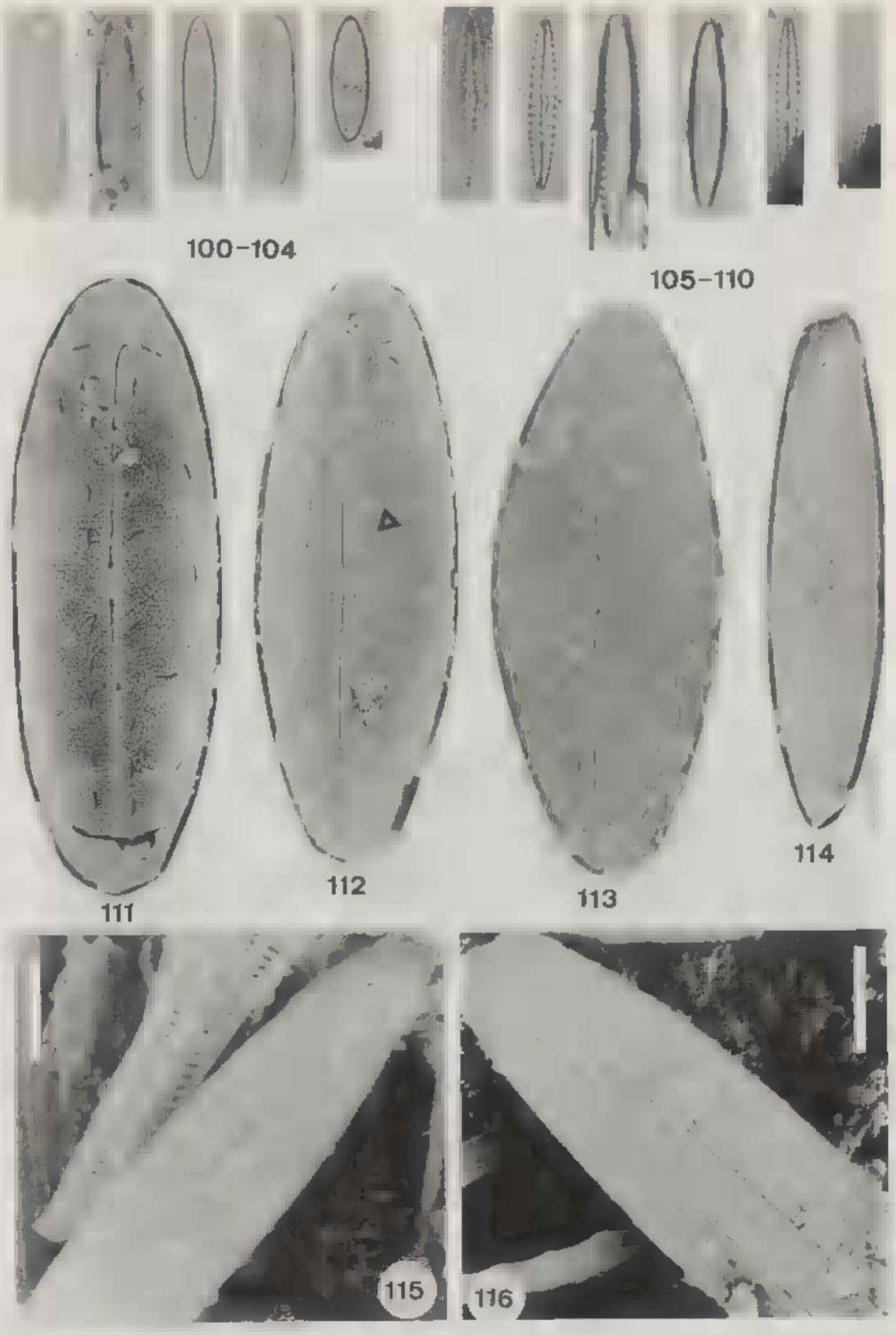


Figs 69-76. SEM. Figs 69-70. *Navicula flagellifera*. Fig. 69. Valve interior showing centrally positioned internal raphe slit which is located within a raised siliceous rib. Fig. 70. Apical part of the specimen illustrated in Fig. 69. showing the internal areola openings the interior of the valve apex. Fig. 71. *Navicula* aff. *retusa*. Valve exterior seen from the girdle side showing a simple, slightly deflected apical raphe ending. Fig. 72. Small *Navicula* sp. valve structure typical of the group around *N. cancellata*, note simple, central internal raphe slits. Figs 69-72. Specimens from the Mississipi Delta. Figs 73-76. *Navicula distans* var. *borealis*. Fig. 73, 75. Apical part of the valve exterior showing external raphe ending. Fig. 74. Apical part of the valve interior. Fig. 76. Valve interior, note the presence of distinctly thickened central nodule (arrowhead). Figs 73-76. Specimens from Bear Island. Scale bars = 5 µm.

Figs 77-81. SEM. *Navicula platyventris* group. Figs 77-78, 80. *Navicula platyventris*. Fig. 77. Valve exterior showing irregular external openings of the arcolae. Fig. 78. Valve interior, note the presence of simple, centrally positioned internal raphe slit, absence of central nodule and the valvocopula with short outgrowths (arrowhead). Fig. 80. Valve interior with hymenate areola occlusions. Fig. 79. *Navicula* sp. Valve exterior with S-shaped external areola openings. Figs 77-80. Specimens from Kok-tao Island, Thailand. Fig. 81. *Navicula tropicoidea*, specimen from Bear Island. Valve interior showing simple centrally positioned raphe internal slits and valvocopula with short outgrowths. Scale bars = 1 μm.



Figs 82-99. Figs 82-87. *Navicula starmachioides* group. Figs 82-86. *Navicula starmachioides*, specimens from the Gulf of Gdańsk. Fig. 86. SEM. Valve external view, note the presence of slightly curved apical raphe endings (arrowhead). Fig. 87. Complete frustule of an unidentified *Navicula* sp. showing the valve exterior and interior. The valve interior shows presence of laterally deflected raphe internal slits. Specimen from the Littorina sediments of the Mecklenburg Bay, core No. 564024. Figs. 88-93. *Navicula rolandii* specimens from the type slide. Figs 94-96. *Navicula* aff. *perrhombus*. Figs 94-95. Specimens from Tonga, Indian Ocean, Tanzania. Fig. 96. Specimen from the coast of Crete, Mediterranean Sea. Figs 97-99. *Navicula perrhombus*. Fig. 97. Specimen from Fiji Islands, Coll. Foged. Fig. 98. Specimen from Eilat, the Red Sea. Fig. 99. Specimen from La Reunion, Indian Ocean. Scale bar in Fig. 83 = 10 µm for Figs 82-85 and 88-99, scale bars in Figs 86-87 = 5 µm.



Figs 100-116. *Navicula wasmundii* group. Figs. 100-104. *Navicula wasmundii*. Figs 100-101. Specimens from Bear Island. Figs 102-104. Specimens from the Kattegat. Figs 102-103. The same specimens photographed at different foci. Figs 105-110. *Navicula syvertsenii*. Figs 107-108. Specimens from Bear Island. Figs 105-106, 109-110. Specimens from Kattegat photographed at different foci. Figs 111-116. SEM. Fig. 111. Valve external view of *Navicula wasmundii* showing the stria structure, specimen from Bear Island. Figs 112-113. *Navicula* sp. Fig. 112. Valve internal view showing centrally positioned internal raphe slits and hymenate areola occlusions (arrowhead). Fig. 113. Valve exterior showing arrangement of the areolae external openings. Figs 112-113. Specimens from Kok-tao Island, Thailand. Figs 114-116. *Navicula syvertsenii*. Figs 114-115. External views at different magnifications, specimen from Bear Island. Fig. 116. External view of valve seen in girdle view, specimen from Franz Joseph Land. Scale bar in Fig. 100 = 10 µm for Figs 100-101, 107, scale bar in Fig. 102 = 10 µm for